

INBREEDING AND CROSSBREEDING IN *CREPIS CAPILLARIS* (L.) WALLR.

BY

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INTRODUCTION AND BRIEF DISCUSSION OF INBREEDING EFFECTS

It is well established that continued inbreeding within a strain or race may produce results harmful to individuals of that race. It is only in modern times, however, that a consistent explanation of the causes of such results has been made. This explanation of the problem has come through carefully planned and executed experiments upon plants and animals and through a recognition of the Mendelian laws of heredity. The most extensive and comprehensive of these investigations is that with maize, started by East¹ in 1905 and now being carried on by Jones, at the Connecticut Agricultural Experiment Station.

Inbreeding is now considered and used as a method by which the hereditary constitution of the germ-plasm can be made evident. Inbreeding, as such, produces no evil results. The abnormal forms that sometimes appear in inbred strains show up because the recessive genes conditioning such forms are present in the germ-plasm. If no such genes are present, no amount of inbreeding can produce them.

The fact that inbreeding produces abnormal forms and reduction of vigor in some species and not in others is due to a condition of the germ-plasm. For example, no such results attend inbreeding in self-fertilized crops like wheat and barley because in them self-fertilization is the normal method of reproduction and such plants are homozygous for all their genes, all the abnormal and weak plants

¹ East, E. M., and Jones, D. F., *Inbreeding and Outbreeding*, pp. 1-285, 46 illus., Philadelphia, Lippincott. 1919.

having long ago been segregated out of the race and having perished in the competition with their more hardy and vigorous sibs.

Maize is a naturally cross-fertilized species, and heterozygosity is therefore the general condition of the germinal material instead of homozygosity, as is the case in self-fertilized species. In this heterozygous condition the genes of recessive harmful characters may be carried along in the germ-plasm under the protection of desirable dominant characters and appear only when the latter are absent. Inbreeding furnishes conditions favorable to the accumulation of these recessive genes in the germ-plasm and for the appearance of the recessive characters in some of the individuals.

The increase in size and vigor observed in the progeny when two different inbred strains, or inbred strains and unrelated non-inbred strains, are crossed is due to the establishment of a heterozygous germ-plasm containing more dominant factors influencing size and vigor than were present in either of the parents. Linkage of such genes to recessive or to dominant genes which influence vigor and size adversely prevents the production of homozygous dominant races. For this reason the vigor noticed in the F_1 is less marked in the F_2 and subsequent generations where segregation and recombination have taken place.

Most of the knowledge of the effects of continued inbreeding and the results obtained from crossing inbred strains have come from experiments on plants and animals under domestication. Such species have been the subject of conscious selection for particular types, which often preserves in the species characters desirable from an agricultural point of view, but so detrimental that the race could not exist except under the conditions of domestication. It has been questioned whether the germinal material of such races is comparable to that of wild species in which natural selection may have largely eliminated from the germ-plasm genes which produce characters detrimental to the natural existence of the species. In view of this possibility the question has arisen as to whether or not the results of continued inbreeding would be the same if wild species, in place of domesticated ones, were the subject of such experimentation. It is in this connection that this report on inbreeding in *Crepis* is of interest.

MATERIAL AND METHODS

Crepis capillaris is a species belonging to the chicory tribe of the Compositae. The species is a native weed of European and North African countries, and has been introduced into both North and South America, where it grows in limited localities as a common weed. It is either annual or biennial. The flowers are all perfect and both cross and self-fertilization take place under natural conditions. In nature it is quite variable in a number of ways according to the environmental conditions in which it grows, but our breeding experiments show that, when grown continuously under the same conditions, constant forms are produced in successive generations. No records have been found of its subjection to extensive artificial selection and it is therefore, in the true meaning of the word, a wild species.

In order to reduce the effect of variation in the environmental factors of soil, light, temperature, moisture, and space to the minimum care was taken to have the soil homogeneous, to have the same size and kind of pots, and to grow successive generations of plants in the same portion of the greenhouse as their parents had occupied. This last item was varied in the last generation (1920) to the extent of placing both inbred and hybrid cultures on a bench on the opposite side of the greenhouse from the side where the parent cultures grew. Inbred and hybrid cultures have been grown side by side. The arrangement in plate 39, figure 1, and plate 40, figure 1, is that in which the plants grew on the bench. Some of the inbred plants and some of the crossbred plants were grown in both four and six-inch pots. This did not alter the size and growth relations in any way.

Crossing was accomplished in cultures 115 and 129 by emasculation² of the plants intended to be female parents, while in H-10 the water² method of depollination was used.

² To be described in detail in another paper.

INBREEDING AND CROSSBREEDING EXPERIMENTS

Cultures of *Crepis* were first grown to study and to isolate certain character variations which had been observed. Forced inbreeding was resorted to as the quickest means of reaching the desired end. After two generations of inbreeding it was noticed that the plants were much smaller and less hardy than at first, notwithstanding the fact that cultural methods had not varied to any marked extent. Experiments were then planned and executed with these cultures to demonstrate the effects of continued inbreeding and subsequent crossing in a wild species, and the results obtained form the body of this report.

In Table 1 are given the pedigrees of the cultures in which inbreeding was continued. Cultures 20.113, 20.114, and 20.128 have identical ancestors previous to their parents, which were sibs. In the second generation of inbreeding, sibs of culture e2 were crossed because the strain showed such a high degree of self-sterility that it was feared that not enough viable seed could be secured to maintain the strain. By crossing sibs, which, however, were very similar in all respects, a few viable seeds were secured. Self-fertilized seeds of e32P₆ and of e32P₁₈ were also secured and their cultures were in all measurable respects no less vigorous than the progeny of crossed sibs of culture e32. Plate 41, figure 1, shows culture 113, derived from crossing sibs, and culture 114, derived from selfing one of the sibs used in the cross. Thus for inbreeding purposes the culture e2 had reached an almost homozygous condition in the third generation, since in no case have appreciable changes been noticed in the fourth generation.

Culture e28 also seemed to reach its maximum reduction of vigor and size in the third generation of inbreeding. No crossbred plants from this inbred strain have yet been grown. In contrast, H-10 (pl. 41, fig. 2), resulting from crossing sibs in the two previous generations, shows but little reduction in vigor or size, indicating that it is either still heterozygous genetically or is not affected by inbreeding to the same degree as e28. The latter seems to the writer more probable, inasmuch as the entire culture of H-10 was fairly uniform, thus indicating a large degree of homozygosity.

Cultures 17.192 and Z9 used in the crossbreeding experiments were chosen because they could have no immediate genetic relation

to the inbred cultures. Seed secured from wild plants in Berkeley, California, was used in 1916 to start the culture 17.192. Cambridge (Quy Fen), England, is the source of culture Z9. The latter were slightly more vigorous than the Berkeley plants. Culture 17.178 was grown from seeds from wild plants found growing near Eureka, Humboldt County, California.

Culture e33, which was used as one of the parents of crossbred culture 129, is a reciprocal of e32, and similar in all respects.

Pedigrees of the plants used in these experiments are shown in the accompanying tables. In Table 1 two systems of symbols are used to designate cultures. In the parent stock and in the first and fourth generations the annual-notebook-page-number system of Shull is used. In the second and third generations individual cultures are designated by key letters combined with numbers. In both tables individual plant numbers are designated by P with a subscript. In Table 2 the same systems are used together with special key letters (H and Z) to designate certain cultures.

TABLE 1—SHOWING PEDIGREES OF PLANTS USED IN THE INBREEDING EXPERIMENT

Parent Stock	Generations of Breeding			
	First	Second	Third	Fourth
17.178P ₆₀	18.18P ₅	e2P _{2×16}	e32P _{6×12}	20.113
17.178P ₆₀	18.18P ₅	e2P _{2×16}	e32P ₆	20.114
17.178P ₆₀	18.18P ₅	e2P _{2×16}	e32P ₁₈	20.128
17.178P ₁₂	18.31P ₉	e8P ₆₂	e28	

TABLE 2—PEDIGREES OF CROSSBRED PLANTS

	17.192P _{7×4}	—204P _{46×27}	—H10	
	17.192P _{7×4}	—204P _{27×6}	—H6P ₈	} —20.129
			×	
17.178P ₆₀	—18.18P ₅	—e2P _{16×2}	—e33P ₆	} —20.115
17.178P ₆₀	—18.18P ₅	—e2P _{2×16}	—e32P ₁₅	
			×	
			Z9P ₆	

DISCUSSION OF RESULTS

One would expect that the germ-plasm of an old wild species had been largely purified of the genes which cause the production of abnormal and harmful characters by the elimination of weak forms through natural selection, but our experience with *Crepis* demonstrates that such is not the case in a race partially cross-pollinated. The germinal material of *Crepis capillaris* is maintained in a heterozygous condition by natural cross-pollination, as is the case in the cultivated species of maize. This is shown first by the marked reduction in the size of the plants and their slower rate of development, and secondly by the fact that we have isolated, by inbreeding and selection, constant breeding forms which differ in the characters for which selected.

The maximum amount of the effects of inbreeding appears to occur in the second and third generations. Forms have been observed in inbred cultures which have not been observed in wild colonies; no doubt a more extended observation would show that they do occur, though rarely. Pollen sterility is one of the results of inbreeding and one plant has appeared in a third generation culture which produced almost no pollen. In the culture produced by growing seed of wild plants which themselves grew in New Zealand we have also found one plant (N. Z. P., 1920) which produces no pollen at all; other plants of this culture appear normal in pollen production. This is evidence that this character may also appear in wild plants.

Strains of fasciated plants have been isolated in *Crepis tectorum* which are so weak that it is only by starting a large number that we can get a few to live long enough to produce seed, yet the plants in the heterozygous condition seem to be in no way affected.

Most of the plants were grown in four-inch clay greenhouse pots. In order to determine whether this limiting of the root space would in any way accentuate the dwarfishness of the inbred plants, part of inbred strain No. 128 and part of hybrid culture No. 129 were grown in both four-inch and six-inch clay pots and placed in adjacent rows on the bench. Plate 40 showing plants in six-inch pots and plate 39 showing similar cultures in four-inch pots answer this question in a very definite manner.

The results of inbreeding in *Crepis* support the statement of East and Jones³ that in naturally cross-fertilized organisms the immediate results of inbreeding are most emphatically injurious, but it must be considered as an exception to their statement that "wild types, in general, might not present such an appearance of injury under inbreeding as shown by cultivated species." Maize is characterized by the occurrence of both cross and self-fertilization, and when this condition exists in wild species we may expect such species to behave like maize when subjected to forced inbreeding.

SUMMARY

Inbreeding in a naturally cross-fertilized wild plant, *Crepis capillaris*, causes conditions in many ways similar to the conditions produced by inbreeding in maize.

The maximum reduction appears to be reached in the third and fourth generations.

Crossing inbred strains with non-inbred strains produces vigorous, rapidly growing F_1 plants.

Inbred plants, when compared with crossbred plants, show a slower rate of development during the entire period of growth.

Some of the inbred strains showed pollen sterility by a reduction in the number of mature pollen grains formed.

Increased size of pots and quantity of soil did not affect the relationship of vigor and of growth.

The results of the experiments on *Crepis* indicate that the results of inbreeding maize as reported by East and Jones⁴ and others are in no way peculiar to that species, but may be found to hold for other species, either domesticated or wild, when similar conditions affecting sexual reproduction obtain.

³ *Op. cit.*

⁴ *Op. cit.*

PLATE 39

Crepis capillaris

Fig. 1. At right and left are plants representing the fourth generation of inbreeding in two related strains.

The central plant is the result of crossing an inbred plant of the third generation with a totally unrelated non-inbred strain of *Crepis*.

Fig. 2. The same three plants as shown in figure 1, photographed about six weeks later, showing the precociousness of the hybrid (115) when compared with the inbred plants.


Plants growing in four-inch pots.



Fig. 1



Fig. 2



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PLATE 40

Crepis capillaris

Fig. 1. 20.129/4. Hybrid secured by crossing an inbred plant with a non-related non-inbred plant.

20.12S/10. Inbred plant of the fourth generation; progeny of the inbred parent of the hybrid plant 129P4.

Fig. 2. The same two plants photographed about six weeks later showing marked vigor of the hybrid.

Growing in six-inch pots.

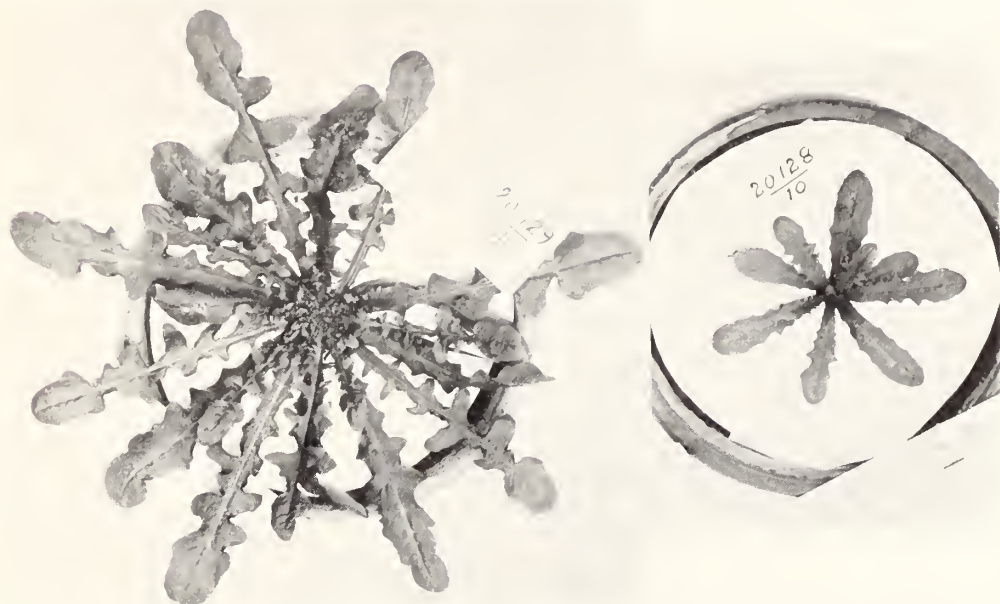


Fig. 1



Fig. 2

PLATE 41

Crepis capillaris

Fig. 1. Cultures 113 and 114 are inbred plants of the fourth generation. Culture 115, F_1 hybrid plants of the same age as the cultures 113 and 114.

Fig. 2. e28/25 and e28/21, inbred plants. H10/11. A non-related plant produced by continual crossing of sibs. Growing in four-inch pots.



Fig. 1



Fig. 2

